

Running Header: magnetic compass use in Damaraland mole-rats

Potential use of a magnetic compass during long distance dispersal in a subterranean rodent

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Geomagnetic sensitivity is present in a variety of vertebrates, but only recently has attention focused on subterranean mammals. We report the potential use of a magnetic compass in wild Damaraland mole-rats (*Fukomys damarensis*) during dispersal at two sites in the Kalahari region of South Africa. When the distance traveled was greater than 250m, males and females dispersed in opposite directions and females preferentially chose a predominantly north-eastern direction. This directional choice likely is due to the differing dispersal tactics between sexes. This evidence suggests that Damaraland mole-rats employ a magnetic compass during above ground dispersal to assist in locating mates or a new territory. This study provides evidence to show how magnetic compass use could be useful in dispersal, an important ecological process for mammals.

Keywords: Damaraland mole-rat, dispersal, *Fukomys damarensis*, magnetic compass, magnetoreception, navigation, subterranean rodent

Terrestrial small mammals rely primarily on visual cues when navigating through their environment (Kimchi et al. 2004). Subterranean mammals have evolved in a micro-environment where visual cues are primarily absent. In African mole-rats, visual acuity is reduced to the point where only changes in light intensity—but no distinct images—are detected (Němec et al. 2007; Kott et al. 2010). Some species participate in seismic communication that transmits low frequency vibrations to their neighbors (Bennett and Faulkes 2000). Their hearing is restricted to low frequencies (Gerhardt et al. 2017) and their ability to localize sound is poor (Heffner and Heffner 1992). Olfactory cues enable subterranean mammals to locate food, mark territories to prevent intrusion, and recognize kin (Heth and Todrank 2007). A large brain area is devoted to processing somatosensory input (Dollas et al. 2019). Because subterranean mammals have burrow systems that are extensive and constantly changing in geometric configuration, they have developed acute spatial orientation abilities and use path integration (or dead reckoning) to find their way around the burrow system (Kimchi and Terkel 2001). Many subterranean mammals across unrelated taxa are able to perceive the geomagnetic field (i.e. magnetoreception) for navigation in their subterranean environment (Moritz et al. 2007; Malewski et al. 2018).

Magnetoreception is defined as the ability to sense or perceive magnetic cues in the local geomagnetic field and transfer information arising from these cues to the nervous system, where the relevant data are interpreted (Moritz et al. 2007). An animal can perceive the strength of the magnetic field (intensity cues), the angle between the magnetic field and horizontal plane (inclination cues), or the direction of field lines pointing to North (polarity or declination cues; Wiltschko and Wiltschko 2005). Intensity and inclination cues provide information enabling the animal to detect where it is in relation to the poles or equator, while polarity cues provide information that assist in goal-oriented travel (Wiltschko and Wiltschko 2005). Migratory birds,

marine turtles, and salamanders orient using an inclination mechanism (Lohmann and Lohmann 1993; Phillips and Borland 1994; Wiltschko and Wiltschko 2005), while bats and subterranean rodents use a polarity-based receptor (Marhold et al. 1997; Wang et al. 2007; Holland et al. 2010). The receptor in bats and subterranean rodents probably is magnetite-mediated, where particles of magnetite in the body align upon receiving geomagnetic cues to provide directional information which assists in goal-oriented travel (Wiltschko and Wiltschko 2005; Moritz et al. 2007). While bats require viewing the sunset for calibration, the receptor of subterranean mammals is completely light-independent (Thalau et al. 2006; Holland et al. 2010).

African mole-rats (Family Bathyergidae) are a family of subterranean rodents endemic to sub-Saharan Africa. They possess the ability to interpret geomagnetic cues received by the cornea and processed by the central nervous system (Němec et al. 2001; Wegner et al. 2006; Caspar et al. 2020) and rely upon this sense during navigation (Moritz et al. 2007). They dig long straight tunnels and their burrow systems often are aligned with respect to a certain axis using a magnetic field as a heading indicator (Malewski et al. 2018). Because mole-rats may travel long distances above ground during natal dispersal (Braude 2000; Patzenhauerová et al. 2010; Finn 2017), magnetoreception has been proposed as an evolutionarily advantageous trait to assist in above ground dispersal (Moritz et al. 2007; Patzenhauerová et al. 2010). To date, only in distantly related mole-rats (Spalacidae: *Spalax*) have magnetoreception navigational abilities been documented during exploratory travel in laboratory maze experiments (Kimchi and Terkel 2001; Kimchi et al. 2004). No studies on wild subterranean rodents have been carried out to assess the possibility of magnetic compass use in navigation during dispersal. In this study, I assess the chosen compass direction of travel in wild dispersing Damaraland mole-rats (*Fukomys damarensis*) to determine if a mean direction of travel is preferred during dispersal. I expect

direction preference to be oriented in one or two directions for all dispersers because of directional preferences in digging and nest building found in previous studies (Marhold et al. 1997; Malewski et al. 2018). In addition, the magnetic field has been shown to influence the directional component of homing and exploratory travel in a distantly related species (Kimchi et al. 2004), a factor that would assist with locating new territories or mates during dispersal.

MATERIALS AND METHODS

The Damaraland mole-rat is a highly social species of African mole-rat inhabiting red soil regions of Namibia, Botswana, and South Africa. They live in family groups of up to 41 individuals with a single reproductive female and up to three reproductive males, while the majority of other group members are offspring of the breeders (Bennett and Jarvis 1988). Both male and female mole-rats remain in their natal group for 1-2 years before dispersing (Finn 2017; Torrents-Tico et al. 2018a). Immigrant males sometimes join groups to gain breeding opportunities (Burland et al. 2004; Torrents-Tico et al. 2018b), while females disperse to a new location, construct a new burrow, and remain alone until an immigrant male joins her (Finn 2017). New groups are formed when an immigrant male finds a single female, by “budding” when a pair (usually an immigrant male and a female group member) take over an infrequently used section of a burrow system, or very rarely when a female finds a lone male. Groups inhabit the same burrow system for multiple generations and make very conspicuous mounds during tunnel construction (Bennett and Faulkes 2000). This site fidelity and indication of activity enables easy recapture of the same groups for longitudinal study as well as locate new groups (i.e. dispersing individuals) within a study area by walking transects.

Damaraland mole-rats at two sites in the Northern Cape province of South Africa, the Kalahari Research Centre (KRC; 26°58'S, 21°49'E) and Tswalu Kalahari Reserve (Tswalu;

27°26'S, 22°16'E), were captured routinely between September 2013 and December 2018 as part of a long-term demographic study (Finn et al. 2018; Supplementary Data SD1). The landscape at both study sites was categorized as arid thornveld acacia experiencing hot summers and cold winters with a rainy season between December and March (Finn et al. 2018).

Mole-rats were captured using modified Hickman traps (Hickman 1979) checked every 2 – 4 hours, and groups were recaptured approximately every 6 months (see Finn 2017 for detailed capture and release methods). Captured individuals were anaesthetized with isoflurane inhalation (Parker et al. 2008) and individuals >20g were implanted with a subcutaneous passive integrated transponder chip (Trovan Unique, DorsetID, Aalten, The Netherlands) to uniquely identify them. Captured mole-rats were housed with their family members at 20 – 25°C in artificial tunnel systems made from polyvinyl chloride (PVC) pipes, provided with a nest box, and given sweet potato and natural food items *ad libitum* (Bennett and Jarvis 1988). After the last animal was captured, a waiting period of 24 – 48 hours passed without activity in the traps to ensure no other group members were present in the burrow as well as no foreign conspecifics invaded the empty burrow (which never happened). After all individuals in a group were captured or after 7 days in captivity had elapsed (mean \pm SD = 3.4 \pm 1.7 days in captivity, n = 424 capture events) all group members were returned to the same tunnel opening in their burrow system. All protocols were approved by the University of Pretoria ethics committee and complied with regulations stipulated in the Guidelines for the Use of Animals in Research (Permit ECO32-13) and Sikes et al. (2016).

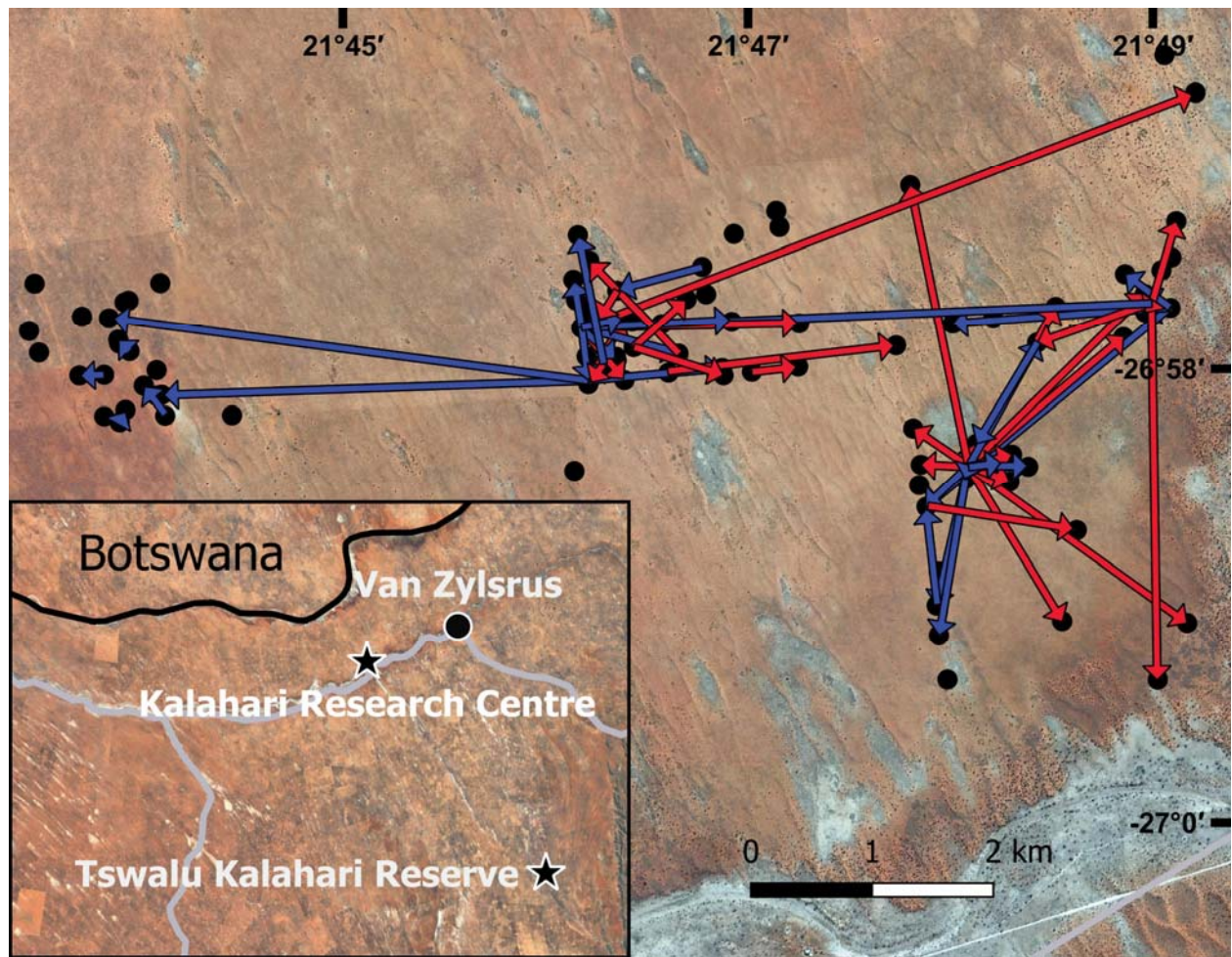


Fig. 1.—Map of the Kalahari Research Centre study site. Arrows indicate emigration from natal burrow to new group/burrow (males – blue, females – red; black dots are mole-rat groups).

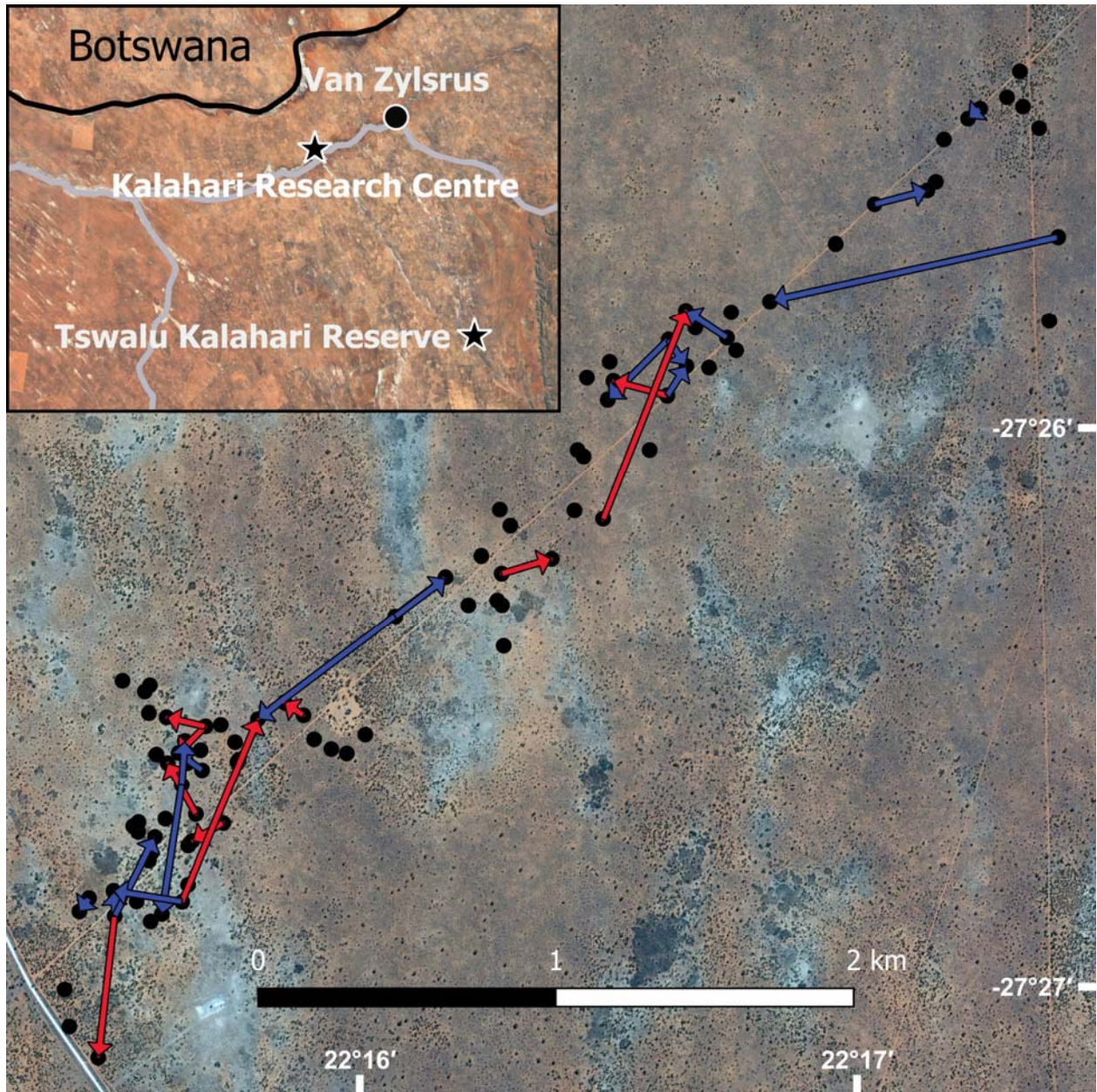


Fig. 2.—Map of Tswalu Kalahari Reserve study site ca. 120km southeast of Van Zylsrus. Arrows indicate emigration from natal burrow to new group/burrow (males – blue, females – red; black dots are mole-rat groups). The white line on the left side is a road which forms the western boundary of the reserve.

During the study period, 937 animals were captured in 119 groups at the KRC, and 702 animals in 94 groups at Tswalu (Figs. 1, 2). Researchers endeavored to capture every group within the two study areas so that all mole-rats in the area could be implanted with a transponder

and their movements monitored. Individual identity was ensured by scanning each mole-rat at capture for a transponder tag. Longitudinal capture data and the presence of different breeding females in each group determined that animals in neighboring groups were independent groups. During the study period, fresh mounds would appear in locations previously lacking mounds, and these fresh mounds indicated new groups. The mole-rats at these new areas were captured and scanned for a transponder tag. Often these new groups were known immigrants that dispersed from their natal group and not animals from the nearest neighboring groups.

Immigrants were marked animals that dispersed from their natal group and were recaptured in a new location (i.e. a different group or newly created burrow). Repeated captures of immigrants at the new locations determined that they remained within the new burrow system without returning to their natal group or other neighboring groups. Thus, the dispersal events presented here are not exploratory in nature.

The dispersal directions of individual immigrants were compared between study sites and between sexes. First, the distance from an immigrant's natal group GPS location to the new group location was measured (to the nearest meter) using the R package *Geosphere* (Hijmans 2019). The distances travelled were log transformed. The immigrants then were divided into two groups, those that traveled < 250 m (short distance) and those that traveled > 250 m (long distance). The distance of 250 m was chosen because individuals could potentially travel that distance underground by digging during favorable conditions, while greater distances would be ecologically costly to dig (Lovegrove 1989) and therefore more likely to be instances of above ground dispersal. The direction of travel (to the nearest degree) was measured in Google Earth and corrected to the location of magnetic North by subtracting the declination for the area based on the year of capture (16° for the KRC and 18° for Tswalu; Thébault et al. 2015). A linear

mixed model (LMM) was used to determine if direction was affected by distance travelled or differed between study sites. Direction was the response variable and location (KRC or Tswalu) and distance were predictors. The residuals of the model were tested for a normal distribution and variance (Supplementary Data SD2). A Rayleigh-test of uniformity was used to assess if the direction of individual immigrants differed from a random distribution for males and females. A Watson-Williams *F*-Test determined if direction during dispersal differed between sexes. All statistical analyses were undertaken in R version 3.6.2 (R Development Core Team 2019) with the package *Circular* (Agostinelli and Lund 2017; Supplementary Data SD2). Data are reported as mean \pm SD.

RESULTS

During the study, 63 immigrant individuals at the KRC (males = 32, females = 31) were captured from 57 groups and 25 immigrants (males = 15, females = 10) from 22 groups were captured at Tswalu. Of these immigrants, 44 at KRC (68.6%; males = 29, females = 15) and 15 at Tswalu (60.0%; males = 8, females = 7) became breeders in their new group. Results from the LMM show that direction did not differ between study location and was unaffected by dispersal distance (Location: *P*-value = 0.96; Distance: *P*-value = 0.55). Thus, data from both study sites were pooled for circular tests. Short distance immigrants travelled $147.2 \pm 52.8\text{m}$ ($n = 30$) and long distance immigrants travelled $1028.3 \pm 933.3\text{m}$ ($n = 58$). Direction of dispersal did not deviate from random, nor was it significantly different between the sexes during short distance dispersal (Table 1). However, there is a noticeable but not significant preference in males for directions between SW and NE ($P = 0.06$, Fig. 3). During long distance dispersal, direction of travel differed significantly between sexes, and directional preference of females was non-random (Table 1). It appears that females dispersed in a predominantly northeastern direction

during longer distance excursions (Fig. 3).

Table 1: Circular statistics results from Rayleigh-test of uniformity and Watson-Williams *F*-Test at two populations of Damaraland mole-rat in the Kalahari region of South Africa.

	Mean Heading	Rayleigh r	Rayleigh <i>p</i> -values	Watson- Williams W	Watson-Williams value	<i>p</i> -
<i>Dispersers <250m</i>						
Males (n = 20)	293° ± 109.5	0.370	0.06	0.926		0.63
Females (n = 10)	124.0° ± 98.9	0.246	0.56	-		-
<i>Dispersers >250m</i>						
Males (n = 27)	245.0° ± 101.2	0.203	0.33	6.954		0.03*
Females (n = 31)	34.5° ± 120.9	0.364	0.02*	-		-

* denotes significance

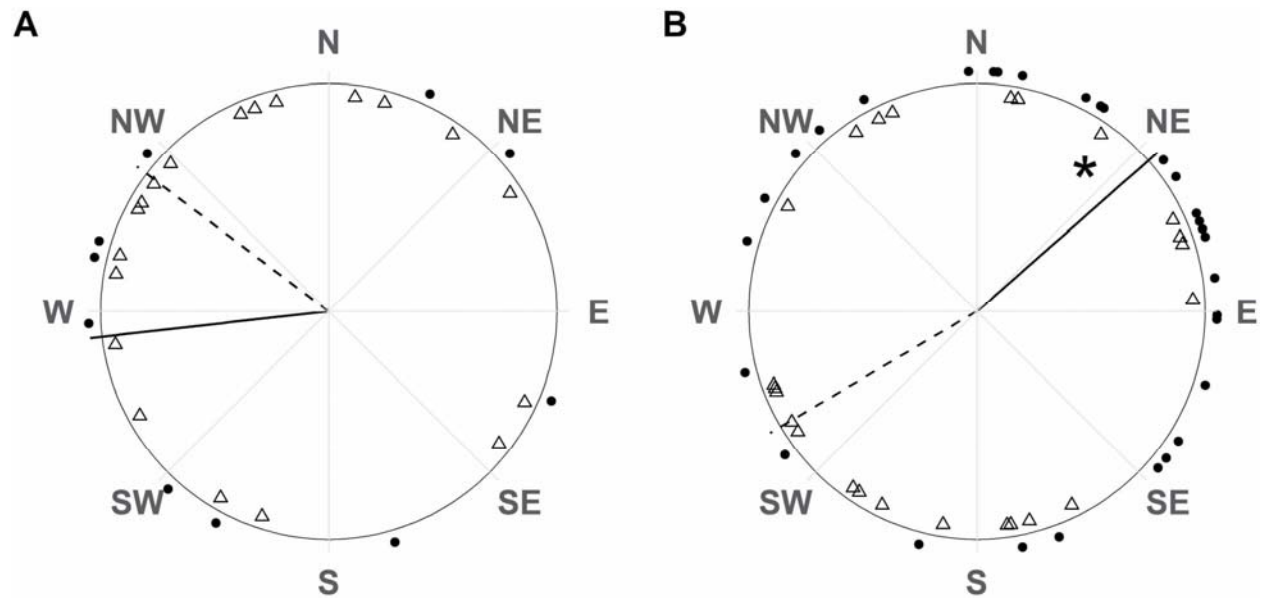


Fig. 3.— Direction of travel from the natal group in immigrant Damaraland mole-rats which travelled a) short distances (<250m) and b) long distances (>250m). Males are represented as open triangles (short distance n = 20, long distance n = 27) and females as filled circles (short distance = 10, long distances n = 31). Mean direction of travel are indicated by dashed lines (males) and solid lines (females). The direction of travel was significantly

different between the sexes for long distance travel only and females significantly preferred a northeastern direction during long distance dispersal (denoted with *).

DISCUSSION

This study provides evidence that the functional use of magnetoreception in subterranean rodents may not be limited to tunnel construction and burrow orientation (Malewski et al. 2018) and may be used during dispersal as previously suggested (Kimchi et al. 2004; Moritz et al. 2007; Patzenhauerová et al. 2010). I expected direction preference to be oriented primarily in one of two directions for dispersing individuals no matter the distance travelled because a preferred direction of digging and nest building has been found in related *Fukomys* species (Oliveriusová et al. 2012; Malewski et al. 2018). The results of my study found that during long distance dispersal, there was a significant difference between the sexes in their direction of travel. Males travelled in a predominantly southwest direction and females in a northeast direction. These directions are surprisingly similar to the burrow orientations reported by Malewski et al. (2018). The similarity in directional choice between these two studies may indicate that an innate directional preference is shared between both digging and dispersal direction. The distances travelled by long distance dispersers would be energetically costly to dig in the narrow window when the soil is soft and workable during the rainy season (Lovegrove 1989). The majority of long distance dispersal instances in this study therefore are likely to have been conducted above ground.

During short distance dispersal, no directional preference was found in either sex, which may imply that below ground dispersal happens more frequently than I expected and could be caused by different orientations of burrow systems (Lovegrove et al. 1992). Some neighboring burrows may occasionally be connected (Šklíba et al. 2012), but repeated captures of groups

without immigrants from neighboring groups suggests that connections between burrows are rare in this area. The results support the work on *Spalax* (Kimchi and Terkel 2001; Kimchi et al. 2004) where magnetic cues were relied upon during longer travel excursions and it is likely that Damaraland mole-rats also may employ a magnetic compass for navigation and spatial orientation during long distance dispersal, but may rely upon path integration for shorter mating trips.

I hypothesized that magnetic cues are relied upon during above ground dispersal due to the reduced visual acuity in members of the species because the magnetic field influences the directional component of homing behaviour (Kimchi et al. 2004). Damaraland mole-rats are obligate outbreeders, which forces both sexes to disperse to secure breeding opportunities (Jarvis and Bennett 1993). Individuals may disperse long distances from the natal group, instead of one sex remaining in close proximity to the natal burrow (Finn 2017). Unlike solitary mole-rats, which return to their home burrow after mate finding excursions (Patzenhauerová et al. 2010), social mole-rats remain in the new group in which they have obtained breeding rights, evidenced by the fact that over half of the immigrants in this study (66.3% total) obtained breeder status in their new groups and did not return to their natal group. The ability to detect geomagnetic cues may be an ancestral trait to facilitate return to the home burrow after mate finding excursions and later adapted for long distance natal dispersal. The mean directional preference during long distance dispersal in females implies it may be more advantageous for them to rely upon a magnetic compass to locate a new territory because females are more likely to construct a new burrow for themselves and await the arrival of an immigrant male (Finn 2017). Magnetoreception may have evolved as a secondary sense due to the poor visual acuity of mole-rats because reliance on magnetic cues would facilitate rapid linear movement to avoid circuitous

routes which would increase digging efficiency or reduce search times for mates during dispersal, thereby also reducing predation risk during these activities.

The lack of a unified direction of travel in males during long distance dispersal is more difficult to interpret. Males are more likely to immigrate into the burrow of an established group to obtain breeding opportunities (Finn 2017; Torrents-Ticó et al 2018b). Many males travelled through or nearby the territories of other groups during long distance dispersal and it is puzzling why they did not stop at these closer groups but instead continued on to their destination. Braude (2000) proposed that males follow scent cues provided by receptive females during mound creation. I speculate that long distance dispersal occurs primarily above ground due to the high energetic costs of digging (Bennett and Faulkes 2000) and mole-rats even have been observed walking on the surface occasionally during the rainy season (Hazell et al. 2000). The scent cues of receptive females in fresh mounds are more likely to be detected on the surface than through the soil. Alternatively, a magnetic compass may be used in conjunction with the other senses. The slightly non-significant directional preference during short distance dispersal may indicate that a magnetic compass is partially involved under certain criteria (i.e., inability to detect a scent from receptive female) and another sensory mechanism is relied upon when those criteria are fulfilled.

The possibility of dispersing mole-rats following dune ridges and valleys during dispersal may be ruled out, because these ridges run predominantly North-South in the Kalahari region. However, it may be that the dispersal direction is mediated by the light provided by the Milky Way or moon, as seen in dung beetles (Dacke et al. 2013), because we observed an east-west direction of travel. Mole-rats may be able to perceive light from the moon (P. Němec, Faculty of Science, Charles University, Prague, Czech Republic, pers. comm. 14 April 2020) and are able to

focus on distant objects (Hetling et al. 2005; Kott et al. 2014), but whether or not mole-rats can actually focus on the moon has yet to be tested.

This study provides evidence that magnetoreception in subterranean rodents may not be limited to nest construction and burrow orientation. The use of bio-loggers has gained popularity in recent years to provide information on spatial behavior (Williams et al. 2020). Bio-logging devices can be equipped with a triaxial magnetometer that orients itself with respect to magnetic north enabling researchers to monitor the animal's heading on species that may otherwise prove difficult or impossible to observe under natural conditions (Williams et al. 2020). Attaching magnetic bio-loggers to subterranean rodents would be a novel method to determine orientation during both tunnel construction or during dispersal events. Alternatively, a less costly experiment involves releasing wild mole-rats in a large circular arena under the natural sky and varying moon phases, similar to the study by Dacke et al. (2013) where the eyes were obscured to test how light affects travel direction. In addition, exposing some mole-rats to Helmholtz coils prior to testing could enable assessment of how changes to the magnetic field affect directional preference (*sensu* Holland et al. 2010). Such studies could remove the confounding influences of lunar bodies and scent cues for directional choice of dispersing mole-rats.

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Supplementary Data SD1.—Regional map

Supplementary Data SD2.—R code used for analysis and raw data

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